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Reassessment of the Platyrhacidae, a family of polydesmidan millipeds

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ABSTRACT

The definition and content of the family Platyrhacidae are reconsidered in light of several recently discovered character systems, and with a critical appraisal of the "traditional" features considered definitive of the taxon. The conclusion is reached that Platyrhacidae sensu Hoffman, 1980, is a composite of three valid families, two of which (Platyrhacidae and Aphelidesmidae) are related by two strong synapomorphies (compound setae and reduced cyphopods), while the third (Euryuridae) is relocated on the basis of a strong synapomorphy (shape of gonapophysis) to a position near the generalized stem of Xystodesmidae + Oxydesmidae, reflecting many similarities with the taxon Melaphinae.

INTRODUCTION

The definition, content, and taxonomic position of the Platyrhacidae have been ambiguous virtually since the name was set up by R. I. Pocock in 1895. The extent of the taxon has been alternately increased or diminished, particularly with respect to inclusion or exclusion of a group of New World species collectively referred to as "euryurines". In recent years, intensified scrutiny of traditional character systems has led to the conclusion that, while synapomorphic traits are not abundant, there is reason to believe that the Platyrhacidae in both its historical and current usages is polyphyletic, its components united by plesiomorphic and/or homoplasic features. The following reclassification is proposed for the consideration of present or future investigators, and certainly not as a *fait accompli* in the mind of its originator.

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HISTORICAL SUMMARY

Prior to 1894, virtually all polydesmidan species were included in the single family Polydesmidae. Those referable to the Platyrhacidae in its current (=1980) sense had been described either in *Polydesmus* or a variety of genus-group taxa such as *Stenonia*, *Platyrhacus*, *Euryurus*, *Odontodesmus*, *Acanthodesmus*, and *Pachyurus* (and not always in the exact sense of those names as originally proposed). The truncated shape of the epiproct appears to have been the usual justification for placement.

The family Platyrhacidae (originally spelled Platyrrhachidae) was proposed by R. I. Pocock in April 1895, to include the single genus "Platyrrhachus". Later (October) in the same year, O. F. Cook proposed an outline classification of Diplopoda, in which he not only recognized Platyrrhachidae with the genera *Acanthodesmus*, *Odontodesmus*, *Platyrrhacus*, and *Trachelodesmus*, but made the first prescient separation of "euryurines" by proposal of the new family Augodesmidae (based on the unavailable name *Augodesmus*) which included *Euryurus* and *Polylepis*. Although *Augodesmus* was never validated by a diagnosis or type designation, it eventually became clear (from specimens labeled under that name by Cook) that he intended it for species later recognized as a genus *Amplinus*. The basis for setting these three genera apart was not specified by Cook, but the significant shared difference from his platyrhacid genera was that of the ozopore structure.

In March, 1896, the family (spelled Platyrhachidae) experienced its first exponential growth in a brief synoptic classification by F. Silvestri. Presented in the form of an indented dichotomous key, that treatment - notable for its indication of type species - recognized ten genera: *Cryptoporus*, *Euryurus*, *Oxydesmus*, *Dicrodesmus*, *Platyrhachis*, *Acanthodesmus*, *Odontodesmus*, *Acisternum*, and *Cyrtorhachis*. That these genera were almost entirely known to an young and inexperienced Silvestri only from the literature, explains the several alien inclusions and incorrect anatomical attributions.

Shortly after the appearance of Silvestri's outline, knowledge of the family experienced a quantum leap in sophistication in Cook's paper "Synopsis of Malayan Platyrrhacidae" (Brandtia, no. 1, 1896), written on May 7, but printed at some indeterminate date later in 1896. While treating only the fauna of the Indonesian region in a terse and unillustrated key format, this paper proposed nine new generic names based on specimens in the Berlin museum and, again in a key format, five additional new names for species described in *Platyrhachus* by Pocock in 1894. Regrettably these two keys were not integrated in any way, which imposed a problem of discrimination upon any user. Cook also noted the existence of Silvestri's three generic names *Dicrodesmus*, *Acisternum*, and *Cyrtorhachis*, as well

as Peters' much earlier *Acanthodesmus*, yielding a total of 18 nominal genera of platyrhacids in the "Malayan" region. In a short terminal essay, Cook recognized a number of additional new species in *Phyodesmus* and *Psaphodesmus*, and proposed to sort the genera known directly to him into four subfamilies based on the generic names *Phyodesmus*, *Taphodesmus*, *Psaphodesmus*, and *Acanthodesmus*. Cook stated his intention to publish a more extended and illustrated account of these taxa, but this plan was never realized, with the result that a really pioneering contribution to the study of platyrhacids remained only an ongoing source of frustration and confusion to subsequent workers for many decades.

Later in 1896, Cook turned his attention to the Neotropical platyrhacid fauna under the title "New American Platyrrhacidae" (Brandtia, no. 12, dated 1 August but apparently published at some indeterminable later time). Although unable to recognize *Platyrrhacus* in a strict sense among his material, Cook again resorted to the key format to propose nine new monotypic genera, all but two of them based on new species. Although gonopod characters were mentioned briefly for each genus, no illustrations were provided and the genera were primarily based upon the peripheral characters of the single type species. Under such conditions it is surprising that more generic synonymy has not so far been established (at present, the names *Cyphorrhacus*, *Spilodesmus*, *Arcydesmus*, and *Barydesmus* are combined as junior synonyms of the last-named). It may be noted that Cook continued to maintain the Neotropical "euryurine" genera as a distinct family.

The "Systema Diplopodum" published by Silvestri in 1897 simply listed all of the generic names that had been included in the "Platyrrhachidae" by any previous author, and mongrelized the taxon by inclusion of the genera *Augodesmus*, *Euryurus*, and *Polylepis*, giving a total of 33 names.

The roster of Indonesian platyrhacids was greatly augmented in 1897, in a treatment by Pocock of the extensive holdings in the British Museum from that region. Pocock tacitly admitted all of the taxa proposed by Cook, and added his own new *Stenoniodes*, *Eurydirorhachis*, *Hoplurorhachis*, *Eutrachyrhachis*, *Diodontodesmus*, *Paradesmorhachis*, and *Polydesmorhachis*. In this paper, Pocock provided small but adequate gonopod drawings and made every effort to coordinate his new genera and species with those set up by Cook one year earlier.

Thus, in a two year period, the number of "platyrhacid" genera escalated from three to 37, a large percentage of them monotypic, and the majority proposed for inadequately described type species. This sudden profusion of genera ended abruptly as the three prolific authors turned away from further platyrhacid studies, and a taxonomic backlash was inaugurated by their successor, a man with diametrically opposed generic concepts.

The great two-volume "System der Polydesmiden", appearing in 1898 and 1899, was an ambitious attempt by Carl Attems to survey all of the polydesmidans then

known, with extended descriptions and elegant lithographic representations of gonopod structure. Being undertaken at a very early period in its author's long career, it reflected an inadequate experience with the rich tropical faunas, expressed in the constraints of a very inclusive taxonomic philosophy. Attems himself later remarked these deficiencies and noted in the light of additional experience that ". . .nobody was less satisfied with the System der Polydesmiden than the author himself."

Attems recognized only a single family Polydesmidae, with 13 subfamilies and several groups of genera which appeared somewhat transitional and were placed between various subfamilies without either belonging to any or having any formal category of their own. Thus *Euryurus* and *Pachyurus* found a place between the Eurydesminae and Oxydesminae, and *Diaphorodesmus, Cryptoporus, Platyrrhacus,* and *Plusioporodesmus* constituted the "Anhang zu den Oxydesminae". At least, the composition of the two groups amounted to an unintentional endorsement of Cook's Augodesmidae and Platyrrhachidae. By merging all of the pre-existing platyrhacid generic names under his *Platyrrhacus*, Attems created a considerable number of secondary homonyms, which he renamed (and which had to be rejected in later years when genera were revived and the homonymies removed).

Although the concept of a group containing "euryurine" taxa was tacitly admitted by both Cook and Attems, such an entity was not carefully examined and formalized until 1909 when Pocock reviewed large segments of polydesmidan classification at several places in the "Diplopoda" accounts in the *Biologia Centrali-Americana.* While acknowledging that the "Platyrachidae" was inadequately defined (by the broadened and/or truncate epiproct) as well as internally heterogeneous (in terms of ozopore structure), Pocock clearly distinguished two primary subgroups as the subfamilies Platyrachinae and Euryurinae. It is nowhere evident in any of Pocock's writing that he was personally familiar with the North American genus *Euryurus*, or whether he simply followed the precedent of its historical association with Mesamerican species he studied for the *Biologia.* Nor, insofar as I can tell, was *Euryurus* known to Attems or other Continental workers who wrote about polydesmidans. On the contrary, there is now every reason to believe that the taxon " Euryurinae" (or, sporadically, "Euryuridae"), retained its Cookian-Pocockian integrity solely by default, that is, nobody critically compared material of its various taxa, nor doubted the validity of the "broadened" epiproct as the autapomorphic descriptor of a monophyletic group. The author of the present review, having examined a far greater diversity of relevant material than all his predecessors combined, is therefore the most culpable for having perpetuated an ancient myth through many papers over many decades.

In the years following 1899, Attems examined a rich variety of mostly tropical polydesmidans, and by 1914 (in *Die Indo-australischen Myriopoden)* had acquired

extensive knowledge about their actual diversity and natural groupings. As regards "platyrhacids", however, he remained true to his earlier concept and offerred a very conservative family defined primarily by the "simple" gonopod structure, and of course, the broad, "shovel-shaped" epiproct. Attems' 1914 family Platyrhachidae contained six genera: *Plusioporodesmus* (now known to be a chelodesmid), *Platyrhacus*, *Euryurus*, *Polylepiscus*, *Polylepis*, and *Amplinus*, without recognition of subfamilies.

The "*Essai sur les polydesmiens*" published by Brolemann in 1916 remains a model of the almost clairvoyant taxonomic perceptions for which he has become reknown, a careful summary of a difficult subject clearly and judiciously explained. His treatment of the the Platyrhacidae (spelled correctly for almost the first time) largely followed that of Pocock, albeit with several internal adjustments. Brolemann preferred to rank platyrhacines and euryurines as tribes of a subfamily Platyrhacinae which in turn was coordinate with a new subfamily Aphelidesminae proposed to reflect the greater gonopod complexity occurring in *Aphelidesmus* and *Protaphelidesmus*. In admitting without prejudice 27 of the previously proposed generic names into his Platyrhacini, Brolemann departed diametrically from the view of Attems, who considered all to be strict synonyms of an omnibus *Platyrachus* in his treatments of 1899 and 1914.

Attems' synopsis of the "Platyrhachidae" in his 1926 "Handbuch der Zoologie" treatment is essentially unchanged from the 1914 version, in terms of generic content and the failure to recognize subfamilial categories. Almost the same may be said for the arrangement in the "Tierreich" (1938), in which the seven genera (except *Aphelidesmus*) are distinguished entirely on peripheral characters, and the vast majority of platyrhacine names are subsumed under *Platyrhacus*.

Apparently the first usage of Euryuridae at the family level (excepting Cook's illegitimate Augodesmidae of 1895) was that of Chamberlin (1918) to cover *Aphelidesmus* in his summary of the West Indian fauna. Chamberlin rarely justified his taxonomic innovations, and did not in that case. In any event, this ranking was thenceforth accepted by all subsequent American students of Diplopoda (and some Europeans, e.g., Jeekel in 1963), again with an exception of the present author's recidivism in 1980 in returning to the system suggested by Pocock, 1909.

In my 1954 summary of the Euryuridae, I proposed the first step in extracting the Nearctic genera from the Neotropical, by suggesting that the nominate taxon Euryurinae be recognized as equivalent to the Aphelidesminae and Amplininae. This initiative was followed in my 1980 classification, although with the three subfamilies downsized to the rank of tribes.

The preceeding review exposes the normal sequence of events during the evolution of milliped classifications: the escalation of an initially informal grouping of genera to family rank, followed by the gradual recognition and denomination of

a variety of subordinate taxa as the number of known species and genera simultaneously increased. Only in 1997, however, did the possibility suggest itself that the family as traditionally conceived might be heterogeneous/polyphyletic, and mandate a fresh appraisal of both traditional characters and some only recently noticed for the first time.

TAXONOMY

CURRENTLY RECOGNIZED "PLATYRHACID" COMPONENTS

Aside some dissention about the affinities of *Aphelidesmus*, there seems to be little controversy about the homogeneity of three fairly recognizable taxonomic groupings which have been united in or placed next to the Platyrhacidae. The basic consideration is the relative hierarchial level to which they should be assigned, which in turn will reflect the phylogenetic status of each group *vis-á-vis* the others. For the purpose of the following discussion, the three generally admitted taxa may be designated informally as

1. Platyrhacines s.s. (= Platyrhacinae sensu Hoffman 1980)

2. Euryurines (three North American genera) (= Euryurini sensu Hoffman 1980)

3. Amplinines (11 Neotropical genera) (= Amplinini + Aphelidesmini sensu Hoffman 1980, but see commentary below, that the latter has priority as a group name.)

EVALUATION OF TAXONOMIC CHARACTERS

Attempts to deduce the polarity of almost any taxonomic character in this group are impeded by the lack of any insights about interrelationships of the families within the Polydesmida, to say nothing of their precise delimitation and content. In the absence of anything more tangible, the "outgroup" will have to be all other families placed in the suborder Chelodesmidea my 1980 classification.

A. "Traditional"

1. *Peritreme*. In all polydesmidans, the ozopores are margined with a thin, erect rim, the thickness of which varies slightly according to family. The platyrhacine condition, a broad smooth polished flattened disk, must be considered a derived state of this character, autapomorphic for the group, whereas amplinines and

euryurines have the generalized condition, a fine thin pore-margin set in a marginal thickening of the paranota.

2. *Paranotal lateral edge.* In most polydesmidans (excepting such highly derived taxa as pyrgodesmids), lateral margins of the the paranota, commencing from a thin elevated rim on the anterior margin, are thickened as a prominent marginal tumidity in which the ozopores are located, set off distinctly from the adjacent dorsal surface of the paranota (Figs. 2, 4). In platyrhacines, the paranota are essentially devoid of any marginal thickness, and the peritreme is displaced dorsomediad away from the lateral edge, an exceptional character state which by out-group comparison must be scored as derived and autapomorphic for this one taxon (Fig. 3).

3. *Epiproct.* One of the primary characters for definition of the Platyrhacidae has been deformation of the epiproct from the subconical shape typical of most members of the Polydesmida into an outline (Fig. 5) variously described as broadened, truncated, tongue-shaped, shovel-shaped, inter alia. ("Il n'est guére d'auteur qui ne distingue à première vue un Platyrhacien à sa forme généralement massive, à ses téguments plus ou moins coriaces *et surtout à la forme dilatée de son prolongement préanal*" [Brolemann, 1916, italics mine]).

Concerning this obviously derived state, two points have long been known but never actually discussed in print. First, that broadening of the epiproct occurs in a number of fairly disparate taxa, e.g., batodesmine and xyodesmine chelodesmids, oxydesmids, and sulciferine paradoxosomatids. In chelodesmids and oxydesmids, especially, there is a demonstrable correlation between broadening of the epiproct and derived states of other body characters: the more "specialized" the animal, the broader the epiproct. This condition is therefore one subject to random homoplasy and cannot be considered as autapomorphic for platyrhacids. It may be recalled that a no-less experienced specialist as F. Silvestri mistook an oxydesmid (which he called *Adontodesmus*) as a platyrhacid. Second, that even within a relatively compact subgroup (subfamily or tribe) the degree of deformation may vary in a continuum from negligible to conspicuous, which is probably why the equally experienced Pocock (1903) failed to realize that *Fontariopsis* - with a scarcely broadened epiproct - was an oxydesmid.

Because of the equivocality of the character, the shape of the epiproct may be considered apomorphic, but with the qualification of being homoplasic, and not synapomorphic among taxa. The qualifier "broadened" will surely have to be replaced by more precise descriptive terms to be taxonomically meaningful. Against the evidence from other systems, I cannot assert that the traditional use of the character is *per se* an indication of common origin for platyrhacines, euryurines, and amplinines.

4 .*Gonopods*. In all three groups under consideration the gonopods are "simple" in the sense that the coxae are not prolonged ventrolaterally beside the prefemoral base nor provided with a dorsal apophysis, and the telopodite uniformly lacks a prefemoral process, is virtually intorsate, and lacks any indication of divisions beyond the prefemur. However, such distinctions are those of *different characters* and must be treated separately. To signalize a platyrhacid gonopod as "simple" is an oversimplification. The telopodite may vary from a uniramous, flagelliform condition to one with as many as five apical branches of various sizes and arrangements. Throughout the chelodesmoid families, all varieties of simplicity may be found which duplicate almost any condition occurring in the platyrhacids. Lastly, a gonopod is composed of various elements which should be considered separately: a coxa may show chiefly generalized features while the associated telopodite may be notably derived. The concept "gonopod" is far too comprehensive: the appendage is actually a complex of individual character systems. Eventually these must be defined and categorized systematically before they are amenable to cladistic usages.

The most striking instance of significant telopodite "complexity" occurs in the Aphelidesminae, in which a 360° torsion of the gonopod acropodite is accompanied by great elongation of the solenomere and its accomodation in an intricately folded and pleated tibiotarsal region. Such a kind and degree of differentiation in this genus (soon to be divided into five genera) seems to justify its isolation in a separate subfamily even if females cannot be easily separated from those of amplinine species.

It should be obvious that evaluation becomes even more difficult if it be admitted that a gonopod can have a "simple" form either prior to evolving something more intricate (thus plesiomorphic), or as the result of secondary loss of pre-existing structures (thus apomorphic). At present, such a form is so internally mutable **and** externally homoplasic, that its value in diagnosis seems compromised.

One character contributing to the overall simplicity of the "platyrhacid" gonopod is the virtually universal absence of a prefemoral process (known only in two Borneo species). But the process is likewise absent in a variety of other families, including notably the genus *Melaphe* which is currently considered to be a generalized xystodesmid, and many Neotropical genera of Chelodesmidae. It is my opinion that the absence of a prefemoral process is a plesiomorphic expression at least in this section of the Polydesmida..

5. *Shape of hypoproct*. The hypoproct in most Polydesmida is roughly triangular in shape, with the acute apex subtended by two small paramedian setiferous tubercles on the margin. In most platyrhacines, the shape is distinctly more trapezoidal, with the paramedian tubercles much enlarged and the margin between them usually straight straight rather than projecting and therefore apomorphic (Fig.

6). Most amplinines show the generalized condition *except* for the genus *Amplinus* itself, which has a platyrhacine hypoproct.

B. "Innovative".

During recent examination of platyrhacid material, a considerable number of characters, previously not utilized in the taxonomy of the group, have been noted and their distribution traced. To the extent that they appear to be useful, some of these characters are discussed below.

6. *Compound setae*. In all species of platyrhacines and amplinines that I have examined for this character, the setae associated with the labrum (and in many cases also the epiproct and legs) are "multiple" in the sense of resembling bundles of finer setae (Fig. 7). As such compound setae are unknown to me in other families of polydesmidans (or diplopods generally), I suppose they must be regarded as some derived condition that is exclusive to the two taxa mentioned. As it is difficult to imagine such a character evolving independently, and at the same positions, in two unrelated clades, I think tuft setae must be regarded as synapomorphic, and the only instance of a derived character shared by amplinines and platyrhacines. There is no trace of modified setae in the euryurines.

7. *Enlarged tibial trichome*. A fine, presumably sensory, seta occurs on the dorso-apical surface of the tibiae in many polydesmoid taxa. As a rule, the seta is not easily distinguished from the adjacent vestiture without special attention and high magnification. In all platyrhacines which I have examined (17 genera from all parts of the group's range), the tibial seta is distinctly enlarged, and placed on a conspicuous, slightly elevated, smooth and polished base, easily seen with 15X magnification (Fig. 8). In these forms, the trichome is invariably erect (tangential to the tibial surface) in contrast to the declivent vestiture, and both longer and finer. This degree of specialization does not occur in other families, and may be considered an autapomorphy of platyrhacines.

8. *Tibial trichome lost*. In some polydesmoid families there is a notable reduction of setation on the podomeres, especially their dorsal surface. In such cases, the tibial trichome is missing as well, and may be regarded as a loss apomorphy for amplinines (I do not regard hypertrophy and loss of a given structure as two extremes of a transformation series, as they would obviously be affected by different selection factors, and therefore treat the two as separate characters).

9. *Basal overlap of hypoproct*. In all platyrhacines known to me, and no other polydesmidans, there is an evident tendency for the hypoproct to encroach or actually overlap on the midventral area of the preceeding ring (Fig. 6, arrow). This derived condition is therefore an an autapomorphy for platyrhacines. It was previously noted by Loomis (1941) as the primary diagnostic character for his new

genus *Proaspis*, obviously because he did not examine material of other genera concerning that point.

10. *Prozonal texture*. The surface of the prozonum in virtually all polydesmidans is essentially "smooth". It was pointed out to me many years ago by C. A. W. Jeekel that one character separating platyrhacines from amplinines was the relatively coarse prozonal granulation in the former, a specialization that I have been able to confirm throughout that group. Similar texture is known to me only in the oxydesmid genus *Plagiodesmus*, surely as a mere homoplasy as no close relationship between platyrhacids and oxydesmids can be detected. This does not, to be sure, detract from the status of granular texture as an autapomorphy for platyrhacines.

11. *Form of stigmata*. Throughout the entire platyrhacine spectrum, the stigmata are enlarged and often modified with flared rims, &c. , in contrast with the small and undifferentiated condition typical of most polydesmidans, and certainly for amplinines Enlargement and modification must be taken as autapomorphic for platyrhacines..

12 .*Gonosternum*. It seems now generally agreed that, since gonopods are derived from the normal precedent structure of ambulatory legs, those which are still most leg-like (e.g., in platydesmids) represent the plesiomorphic condition. In this context, retention of the median sternal element is ipso facto the generalized state in any milliped order. In polydesmidans, the nearest approach to the original appearance of a sternum that surrounds the coxal bases, with sternal apodemes and stigmata identifiable, occurs in various genera of Chelodesmidae and Oxydesmidae. Prominent median sternal sclerites are plesiomorphically present in amplinines and euryurines; their loss from platyrhacines is autapomorphic for Platyrhacidae.

13. *Shape of male gonapophyses*. In most polydesmidans the vasa deferentia debouch flush on the ventral surface of the coxae of the 2nd pair of legs of males. Development of an elevated rim,ventrally projecting cone, or similar modifications constitutes a sequence culminating in the elongated, apically fringed gonapophysis typical of rhachodesmids and sphaeriodesmoids. I do not consider this progression a transformational series as it has probably evolved independently in several major clades within this order, associated with specializations in other character-systems. Whereas the gonopore is unmodified in platyrhacines and amplinines, presumably the plesiomorphic condition in Chelodesmidea, in the Nearctic species of euryurines there is a long, cylindrical, apically boletoid gonapophysis (Fig. 9) on which the gonopore is located apically. It is duplicated almost exactly amongst genera of the likewise Northern Hemisphere family Xystodesmidae. While such similarity might, taken alone, be justly regarded as a mere parallellism, the possibility of phylogenetic affinity is supported by a close similarity in the gonopods of *Euryurus* and those of species of *Melaphe*, a genus of east-Mediterranean millipeds considered to be

generalized xystodesmids. There is further a close proximation in body form between the two genera mentioned (Figs. 1 & 2), although here the possibility of plesiomorphy is perhaps more likely.

14. *Structure of cyphopods.* I am much indebted to Dr. R. M. Shelley for sharing with me his discovery that in platyrhacines, the cyphopods - normally large, strongly sclerotized, and conspicuous in most polydesmidans - are reduced almost to the point of loss. Some careful dissection is required to detect small, thin, sclerotic areas at the distal end of the oviducts. The same condition obtains also in the amplinines that I have checked, and in which the sclerotized areas are actually withdrawn inward by an invagination of the oviductal aperture. The similarity thus provides an exceptionally strong synapomorphy of these two groups, and stands in striking contrast to the "normal" condition in euryurines in which the receptacle, valves, and operculum are present in normal size and configuration.

RECLASSIFICATION

Family Platyrhacidae Pocock, emended

32 nominal genera in the Indoaustralian region and the Cordilleran ranges of tropical America. Currently, the following tribal groups are recognized:

Platyrhacini (Extreme southeastern Asia, Greater Sunda Islands)
Polydesmorhachini (Philippine Islands: Palawan)
Phyodesmini (Borneo)
Psaphodesmini (Indonesia, east of Wallace's Line)
Barydesmini (Tropical America)
Psammodesmini (Tropical America)
Hoplurodesmini (Borneo)

Known (but so far undescribed) species from southeast Asia (Platyrhacini) are strikingly similar in gonopod structure to many Neotropical forms assigned to the Barydesmini, whether from common origin or homoplasy remains to be worked out.

Family Aphelidesmidae Brolemann, new status

Trachelorhachidae Silvestri, 1898, Silvestri, Boll. Mus. Zool. Univ. Torino, 13 (324): 5.

Aphelidesminae (as subfamily of Platyrhacidae) Brolemann, 1916, Ann. soc. Entom.France, 84: 550. – Pocock, 1909, Biol. Centr.-Amer., Diplopoda, p. 157. – Hoffman, 1954, Journ.Washington Acad. Sci., 44: 57.

Aphelidesmini Hoffman, 1980, Classification of the Diplopoda, p. 164 (as tribe of Euryurinae).

My present concept of this family group entails its subdivision into two taxa, here regarded as subfamilies, distinguished by details of gonopod structure. One of these groups (Amplininae) has been revised by Vohland (1999, in press), the other is currently being worked up for publication by me.

Aphelidesminae (*Aphelidesmus* and three undescribed genera).

Amplininae (*Amplinus*, *Pycnotropis*, *Seminellogon*, *Polylepiscus*, *Varyomus*, *Colomborus*, and five new genera)

The family group name Trachelorhachidae was monobasic with the new genus *Trachelorhachis* Silvestri, 1898, a senior synonym of *Aphelidesmus* Brolemann. Silvestri's name was subsumed under Brolemann's by Attems as long ago as 1914, before the respective dates of publication were known, and in any event cannot be considered the basis of a family name since it is preoccupied by *Trachelorhachis* Agassiz, 1846 (Coleoptera).

Family Euryuridae Pocock, new status

Euryurinae Pocock, 1909, Biol. Centr.-Amer., Diplop., p. 149 (name only, content equivalent to present Aphelidesmidae)

Euryurini Brolemann, 1916, Ann. soc. Entom. France, 84: 584 (as tribe within Platyrhacidae).

Euryuridae Chamberlin, 1918, Bull. Mus. Comp. Zool., 62: 249. – Hoffman, 1954, Journ. Washington Acad. Sci., 44: 57.

Euryurini Hoffman, 1980, Classification of the Diplopoda, p. 164.

I believe the point has been adequately made that in its present conception, the Euryuridae is not even a sister-group of the preceeding two collectively, and the totality of its characters rather imply a kind of "xystodesmoid" taxon, with secondarily modified epiproct. Inspection of various components of the Xystodesmidae reveals a remarkably close similarity with members of the taxon presently called Melaphinae in most peripheral characters (except for the broadened epiproct) and gonopod structure (except that the cannula is set in a marginal notch of the gonocoxa rather than in a socket distinctly removed from the edge as in all xystodesmids). It is now tempting to think of euryurines, melaphines, and some generalized oxydesmids (e.g., *Fontariopsis)* as very closely related representatives of a common ancestor.

Biogeographic Considerations

An association of Euryuridae and Melaphinae is consistent with extensive precedents in many animal and plant taxa, whose modern distributions strongly reflect previous, preatlantic, continuity between eastern North America and the Mediterranean region. As a point in fact, I commented already in my 1978 revision of *Euryurus* that "The affinities of *Euryurus* and *Auturus* to Neotropical members of the Euryurinae remain uncertain, but the North American species might be regarded as generalized survivors of an extensive Tertiary platyrhacoid fauna dispersed throughout the Holarctic region." This was an entirely intuitive perception, but proved predictive of this more objective analysis, and is still satisfactory if the the word "platyrhacoid" is omitted!

A shared origin of Xystodesmidae and Oxydesmidae in the Palearctic region was discussed at some length in my revision of the latter family (1990: 17-18) and such a cradle is not inconvenienced by the addition of early forms of euryurids.

However, if the proposed relocation of Euryuridae is biogeographically plausible, a major problem remains with respect to its erstwhile "relatives". Firstly, what might constitute a reasonable sister-group for the combined Platyrhacidae+Aphelidesmidae? Secondly, how may the distribution of Platyrhacidae be accounted? By virtually **all** of the characters whose polarity I can reasonably assert, Aphelidesmidae scores as by far the more generalized of the two taxa. Its area of greatest generic diversity lies in the Cordilleran region of northern South America, with two areas of specific proliferation, namely Mexico (*Amplinus)* and the Amazonian basin (*Pycnotropis*).

The Platyrhacidae occupies essentially the same Neotropical range, although not extending so far northward. But despite qualifying as highly derived in most of its characters, this family occurs also in southeast Asia and most of the East Indies, with a far greater generic diversity than in South America. If platyrhacids were indeed derived from an aphelidesmine-type ancestor, it seems almost necessary that the progenitor group also occured in Indonesia, and later became extinct there. It will doubtless remain speculative until the Platyrhacidae has been revised in sufficient detail that we can establish its probable center of origin.

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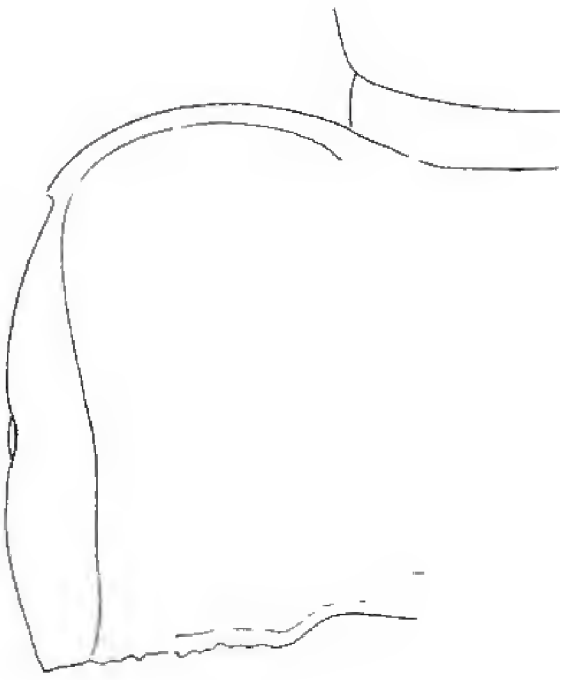

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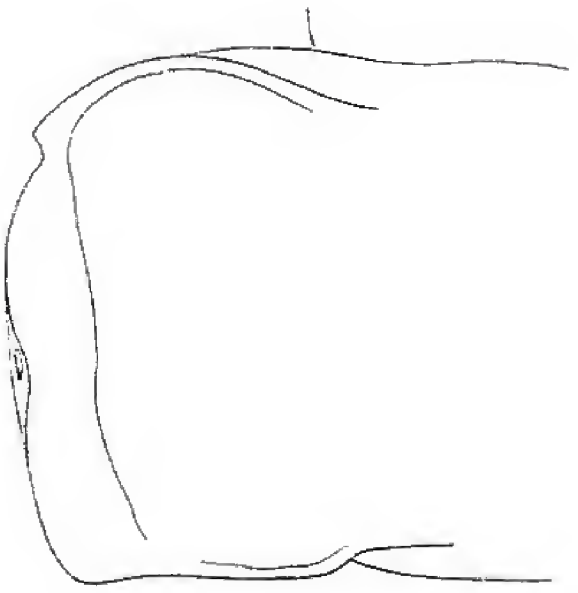

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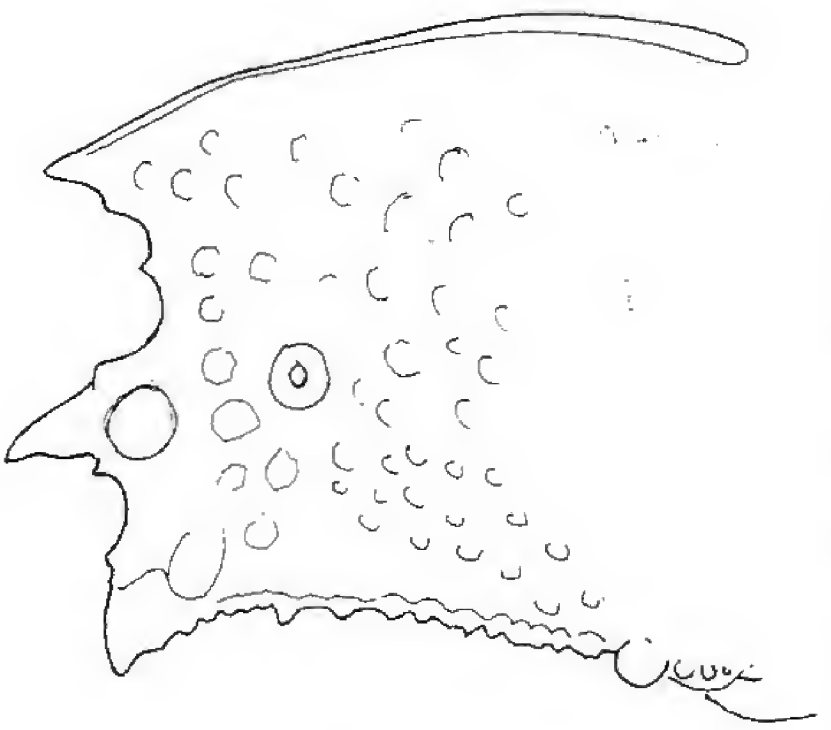

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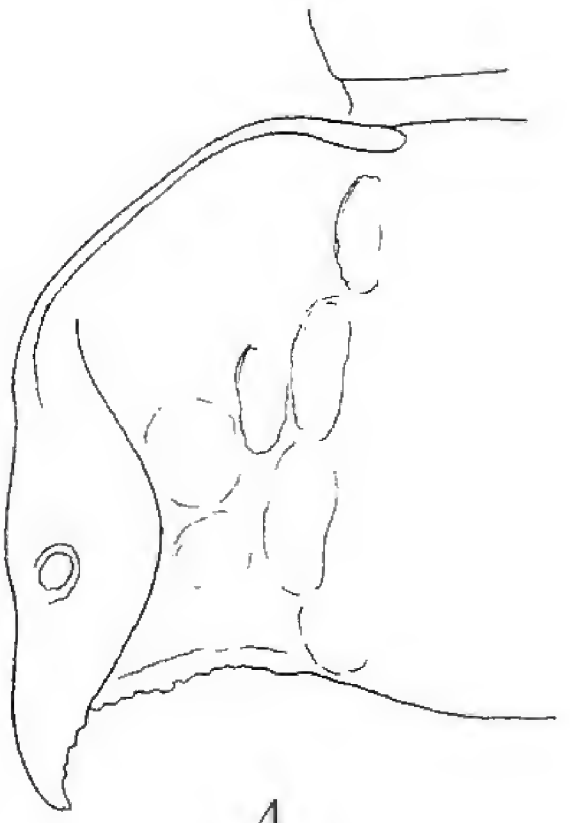

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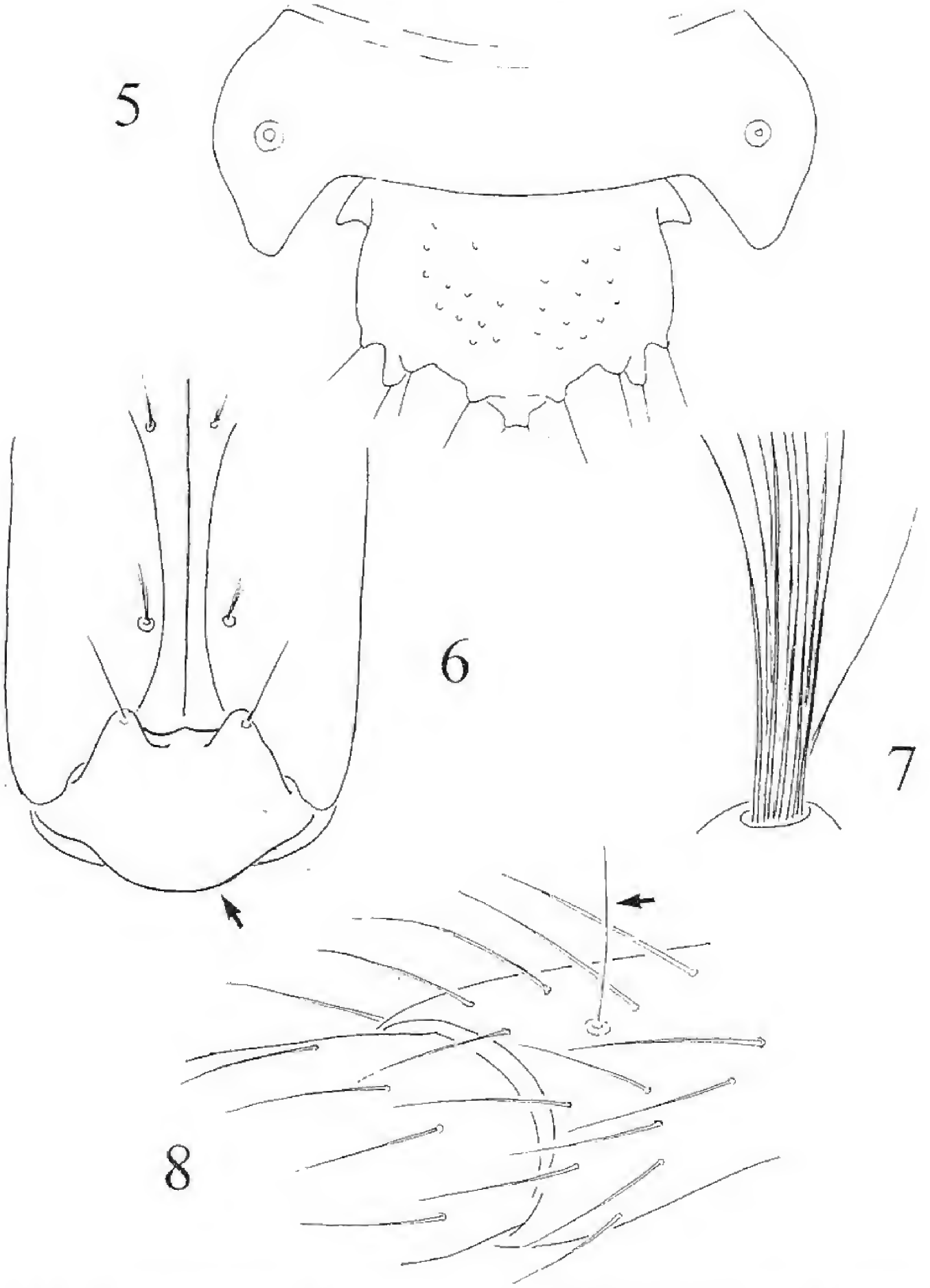
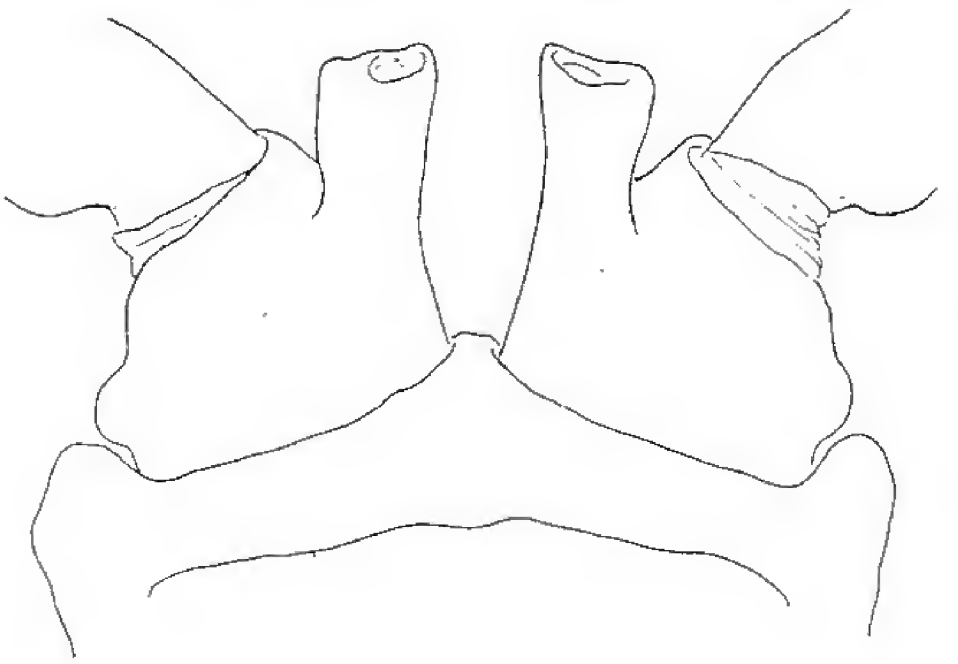
Figs. 1-4, Left paranota of midbody segments, showing variation in ozopore location and presence or absence of marginal peritrematic thickening. 1, *Euryurus leachii* (Gray); 2, *Melaphe vestita* (C. L. Koch); 3, *Barydesmus* sp.; 4, *Pycnotropis (?) abstrusus* (Karsch). Not all platyrhacids have the strongly dentate paranota shown here, but the form and position of the ozopore is characteristic.



Figs. 5-8. Structural details in the Platyrhacidae. 5, posterior end of body, dorsal view, showing broadened configuration of epiproct; 6, anal segment, ventral view, showing basal half of paraprocts, also enlarged paramedian tubercles and basal overlapping lobe (arrow) of hypoproct, the latter an autapomorphy for the family; 7, multiple seta from epiproct, after drying and teasing to separate individual setae, which otherwise adher closely to resemble a single robust macroseta; 8, tibiotarsal articulation of midbody leg, dorsal aspect, showing enlarged subapical trichome (arrow) placed on distinct basal tubercle.



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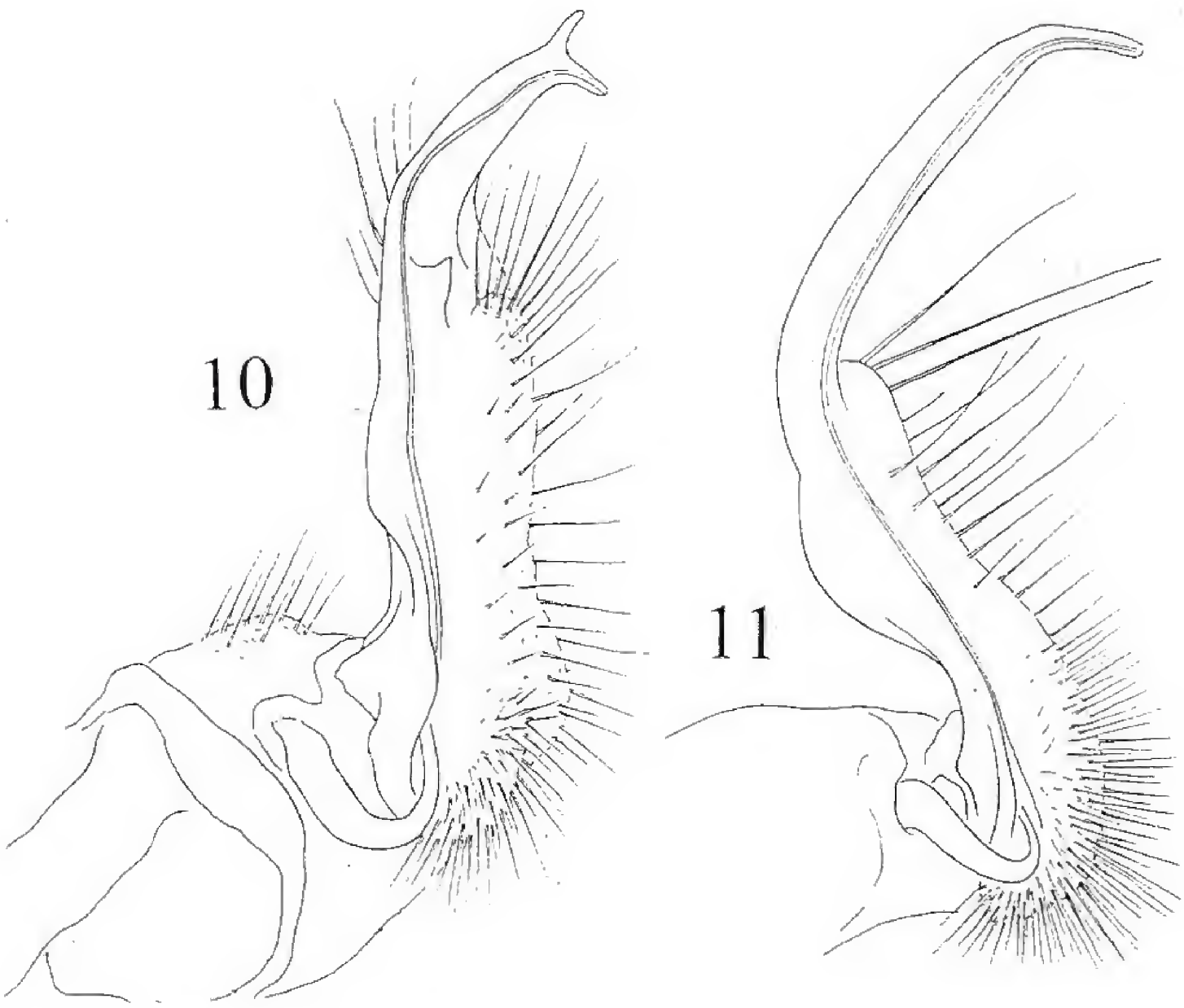

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Figs. 9-11. Male sexual characters . 9, *Euryurus leachii,* sternum and coxae of 2nd pair of legs, showing elongated, cylindrical gonapophyses considered to be possibly synapomorphic for Euryuridae and Xystodesmidae; 10, *E. leachii,* left gonopod, mesal aspect, showing similarity with that in Melaphinae (at least one species of *Euryurus* even lacks the small subterminal process); 11, *Melaphe vestita*, left gonopod, mesal aspect.